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An investigation into the absence of the great white shark (*Carcharodon carcharias*) from British waters

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Abstract

In the last ten years, there have been over 100 reports of great white sharks (*Carcharodon carcharias*) in British waters, yet there has never been a confirmed sighting. British waters are home to the largest grey seal population in Europe and is less than 200 miles away from a known great white population. This coupled with the shark's global distribution and preference for more temperate waters has left many wondering why there has not been a confirmed sighting of this species. To examine the suitability of British waters, four white shark's migrations were mapped spanning nine years. Species distribution modelling through boosted regression trees was then employed to assess the habitability of British waters. The results of this report showed that British waters display near-perfect habitat suitability for both sexes year-round, thus indicating that there is no environmental reasoning for their apparent absence. Despite this, an answer may have been found within their behaviour. When comparing the tagged shark's migrations with what we know about their migratory habits, it was concluded that if a great white were to visit British waters it would most likely be a male from the Mediterranean population swimming at depth, therefore explaining why despite perfect conditions, they have not been confirmed in these waters due to their prolonged time at depth. Alternatively, a counter hypothesis was also put forward, indicating that British waters are suited to the northwest Atlantic population and that the Mediterranean white sharks have different environmental preferences due to their geographic isolation and potential speciation. Recommendations for future research into this highly cryptic species were also made, such as the continued use of satellite tags that record depth and positioning data at all times.

Keywords: Investigation, British, Great white shark, *Carcharodon carcharias*, mapping, prediction, modelling, regression, tagging, tracking, OCEARCH.

Introduction

Carcharodon carcharias

The phylogenetic class Chondrichthyes (fish with a skeletal structure comprised of cartilage) have inhabited this planet for over 400 million years (Camhi, 1998). Due to their trophic position and evolutionary success, it can be argued that a majority of the top-down predatory pressure has come from this class (Estrada *et al.*, 2006). Within this class are two sub-classes, one being Elasmobranch; comprised of Sharks, Skates and Rays, and the other being Holocephali, comprised of Chimaeriformes. *C. carcharias* is an Elasmobranch within the family *Lamnidae*, meaning they can elevate their internal body temperature to roughly 5° C warmer than the surrounding waters, utilising counter-current blood flow (Carey and Teal, 1969); this evolutionary trait grants access to much colder waters.

The Great White Shark (hereafter abbreviated to GWS) is the largest and one of the most widespread extant predatory shark species (Compagno, 2001), inhabiting tropical & polar waters in both hemispheres. GWS's prey on a wide range of taxa, changing their preferences as they mature (Estrada *et al.*, 2006). This change of diet coincides with a change in habitat preference, although it is not known which factor dictates the other. *C. carcharias* were once thought to be a mainly coastal dwelling species (Compagno, 1984), but this is no longer supported as adults have been recorded spending most of their time in the pelagic environment (Boustany *et al.*, 2002; Bonfil, 2005; Weng, 2007; Nasby-Lucas *et al.*, 2009; Jorgensen *et al.*, 2010) and juveniles residing in more coastal environments (Bruce and Bradford, 2012; Skomal *et al.*, 2017). *C. carcharias* is a migratory species, making oceanic voyages of over 20,000 km and displaying the fastest return migration of any swimming fauna (Bonfil, 2005). Furthermore, the GWS is a philopatric species, showing signs of site fidelity (Klimley, 1984; Bonfil, 2005).

C. carcharias reproduction is viviparous, meaning the young gestate inside the womb and are connected via an umbilical cord as opposed to oviparous (egg laying) or ovoviviparous (internal egg). While still in the womb the young display oophagy (Sato *et al.*, 2016), meaning the most developed pups eat their unborn/ less developed siblings; this results in GWS only birthing 1-2 pups per pregnancy (Wourms, 1977). When born, pups are between 120cm and 150cm total length (Francis, 1996), but once mature, they range in size dependent upon sex - males reach ~4.5m and females ~5.5m (Randall, 1973). The largest accurately recorded specimen was a 6.1m female caught in 1984 off of Western Australia (Castro, 2012). GWS are estimated to live 50-60 years (Bruce, 2008) with slow growth rates. Males become sexually mature at 3m and females at 4m (Francis, 1996). This slow development coupled with a gestation period of 12-18 months (Mollet *et al.*, 2000) makes them extremely vulnerable to fishing efforts (Francis, 1996).

British waters

For the purpose of this report, British waters shall be defined as any seas or saline waters situated between -16.070W, 48.144N: 2.722W, 61.188N, depicted in Figure 1. Great Britain lies within the northern hemisphere and has a temperate climate, resultantly having seasonal changes in water temperature. Sea Surface Temperature (hereafter referred to as SST) ranges between an average of 8-11°C in winter, to 16-17°C in summer; with the annual mean lying between 12-14°C.

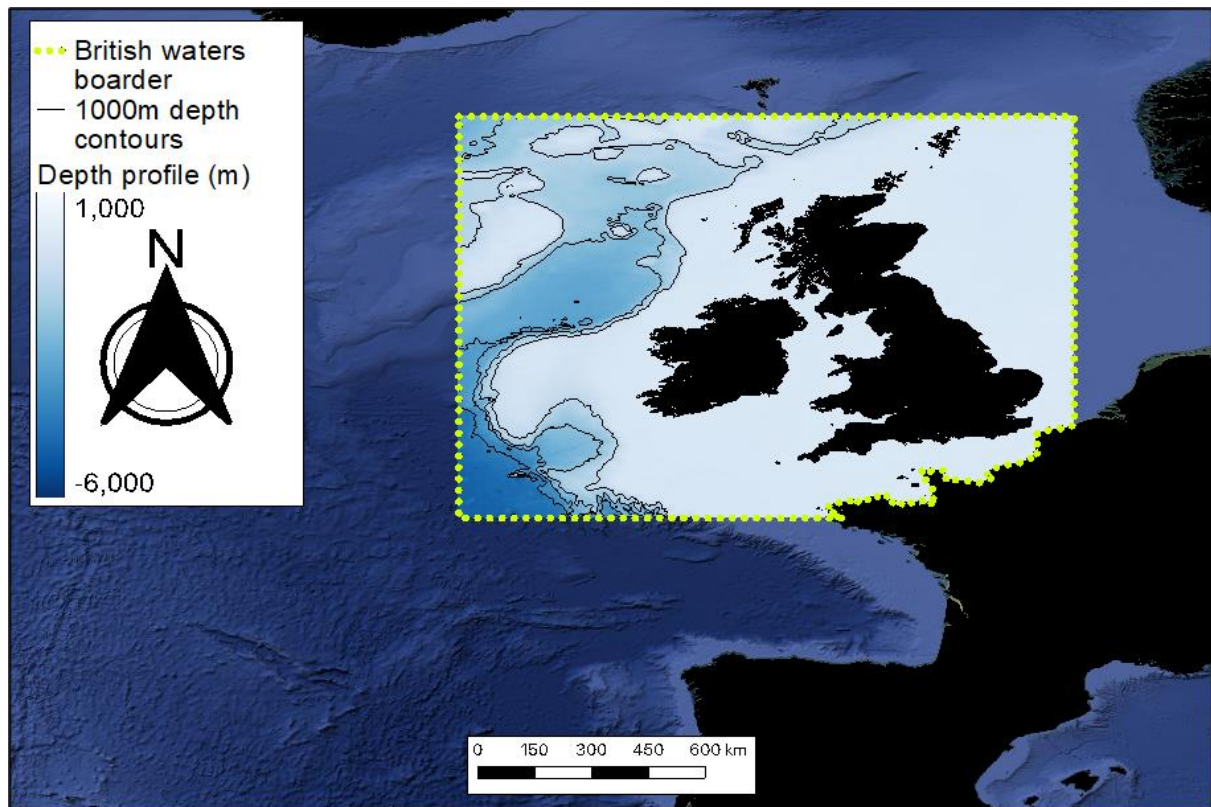


Figure 1: Map of the defined study area referred to as “British waters” with bathymetric data and 1000m contour lines. Data sourced from NOAA.gov.ETOPO1 (Amante and Eakins, 2009). Created in QGISv3.18.

These waters are currently experiencing a slow rise in average SST (Li, Xu and Wan, 2020) as illustrated in Figure 2. British waters as defined for this report, span a latitude of 13 degrees, displaying a north-south SST difference of ~3°C in winter and ~6°C in summer as seen in Figure 3. These waters have a stable and predictable salinity concentration, with values ranging between 35.6ppm and 35.7ppm, dropping near coastal regions due to freshwater discharge from lakes and estuaries (Tiedemann *et al.*, 2014).

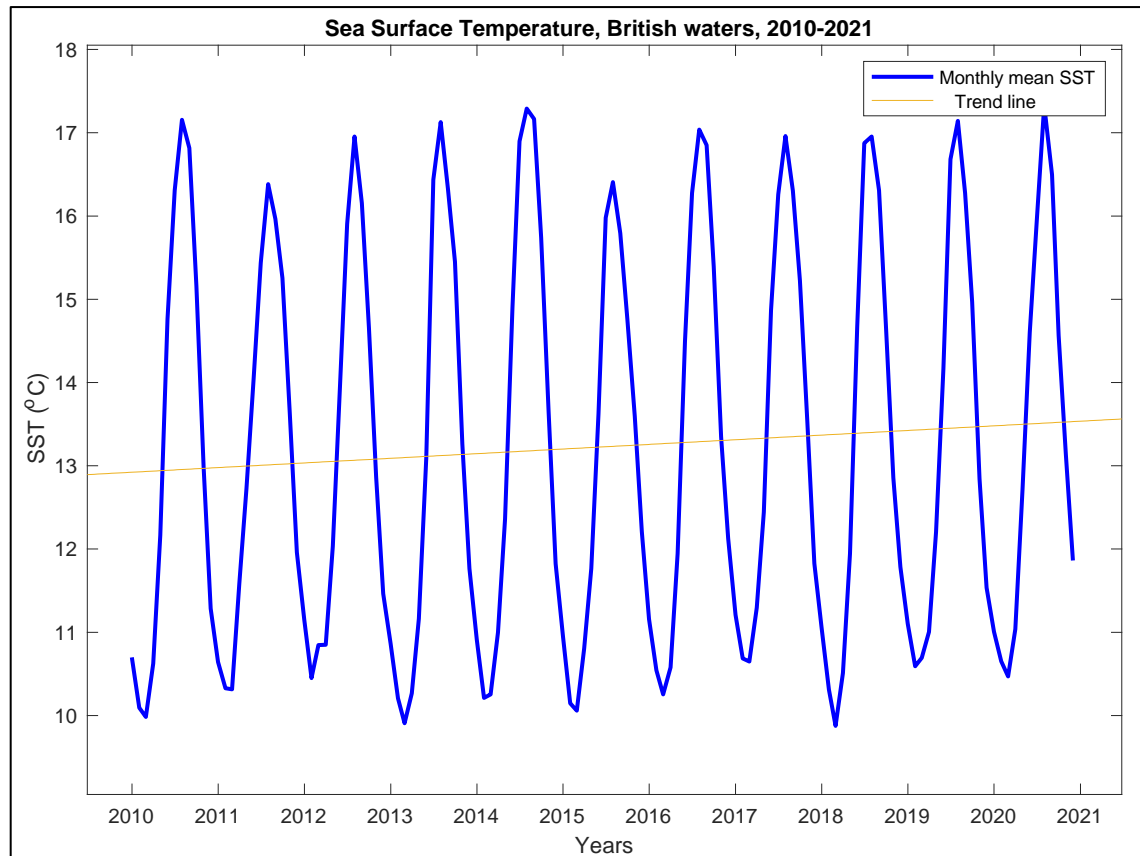


Figure 2: Graphical depiction of the mean range in SST for British waters between 2010-2020, fitted with a trend line. MODIS-Aqua SST data obtained from the NASA Giovanni portal.

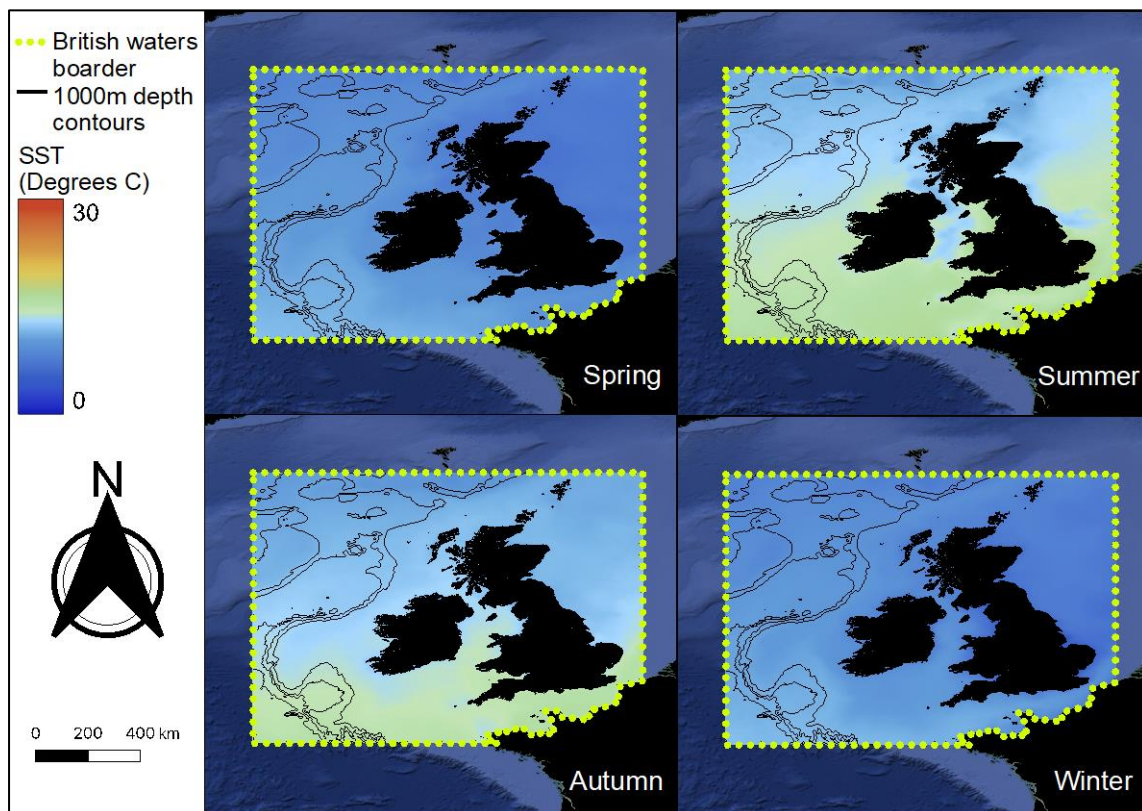


Figure 3: Graphical depiction of British water's seasonal SST averaged from 2010-2020. SST obtained via MODIS-Aqua from the NASA Giovanni portal visualised in QGISv3.18

The bathymetric makeup of the study area for the most part is homogenous as a large portion is situated on the European continental shelf (Mansurbeg *et al.*, 2008), rarely exceeding 150m depth (Roberts, Hunter and Laughton, 1979) - for this reason, these waters are predominantly classed as epipelagic (Choy *et al.*, 2019). On the other hand, the western portion of the study area contains a shelf break with mesopelagic and abyssal waters reaching depths >4000m (Figure 1; Choy *et al.*, 2019). This variety in bathymetry means that British waters experience a wide range of oceanographic events. Waters in the east experience periodic pycnocline mixing; a result of 80% of the water column being vertically stratified for the summer months (Polton, 2022) whereas waters in the west are more mixed due to deep water coastal upwellings and mixing fronts (Palmer, Inall and Sharples, 2013) facilitating a wider variety of marine biota (Hosegood *et al.*, 2019).

These oceanographic features coupled with varying bathymetry result in waters that are highly primary productive due to the consistent abundance of nutrients in the euphotic zone (Sigman and Hain, 2012). Furthermore, this primary production supports an intricate and diverse food web, allowing British waters to facilitate a wide range of ecosystems and species from cold water coral (Freiwald *et al.*, 2004; Roberts *et al.*, 2009) to large pelagic species such as blue sharks (*Prionace glauca*) (Carey, Scharold and Kalmijn, 1990) and humpback whales (*Megaptera novaeangliae*) (Charif, Clapham and Clark, 2001). British waters are also home to one of the largest seal populations on the planet (*Wildlife Trusts*, no date), with over 43,000 harbour seals (*Phoca vitulina*) (Blanchet *et al.*, 2021) and 90,000 grey seals (*Halichoerus grypus*) (Loneragan *et al.*, 2011). This abundance attracts many predatory shark species such as blue, mako, thresher and port beagle (Drake, Drake and Johnson, 2005).

Literature review: *Carcharodon carcharias*' migration and habitat selection

The GWS is arguably the most famous marine predator on the planet, yet it is almost ironic how little we know about this species, especially in regard to their migration and habitat selection. It is currently believed that temperature and thermal triggers are the main drivers of GWS migration and habitat selection (Carey *et al.*, 1982; Goldman *et al.*, 1996; Pyle *et al.*, 1996; Nasby-Lucas *et al.*, 2009; Domeier and Nasby-Lucas, 2012; Curtis *et al.*, 2014; Skomal *et al.*, 2017), yet some reject this theory (Goldman *et al.*, 1996; Bruce, Stevens and Malcolm, 2006). Research conducted by Curtis *et al* (2014) & Skomal *et al* (2017) implemented the methodology of tagging GWSs with satellite tags to track their spatial-temporal movements across a 3D environment spanning multiple years. They observed GWSs making a latitudinal shift north to waters between ~40°0'0 - 40°5'0"N; although some were recorded at latitudes of 51°0'0"N. These northern migrations coincided with the arrival of warmer summer months. Similarly, the sharks were observed migrating south in the winter months. This temperature-driven migration has also been witnessed in the Indian Ocean (Bonfil, 2005), Pacific Ocean (Weng, 2007; Nasby-Lucas *et al.*, 2009; Jorgensen *et al.*, 2010; White *et al.*, 2019) and the Mediterranean sea (Fergusson, 1996; Boldrocchi *et al.*, 2017). These global observations have led to the general acceptance that seasonal temperature change is one of the governing factors of GWS migration.

Despite this assumption that GWS's move to stay within an optimum temperature range, *C. carcharias* have been well documented across a wide range of

temperatures ranging from 2.7°C to 27°C (Fergusson, 1996; Domeier and Nasby-Lucas, 2008; Bruce and Bradford, 2012; Francis *et al.*, 2012; Skomal *et al.*, 2017) as seen in Table 1. Interestingly this range in thermal exposure is mainly observed in sexually mature individuals, leading to the theory that GWS's experience an ontogenetic shift in temperature acceptance/ resilience (Bruce and Bradford, 2012; Skomal *et al.*, 2017)

Table 1: Tabulation of all temperature ranges recorded by GWSS outfitted with pat/spot tags.

Geographical population	Observed temperature range (°C)
Mediterranean	7.5 – 25
Pacific	6.6 – 23.1
Australia	14 – 22
New Zealand	2.7 – 23.8
Guadalupe	15 – 23.1
Northwest Atlantic	11 - 27

Ontogenesis is the metamorphic process in which an organism's biology or behaviour alters as they mature. In the case of *C. carcharias* this has been noted in diet (Estrada *et al.*, 2006), and migration (Estrada *et al.*, 2006; Jorgensen *et al.*, 2012).

The GWS was not first thought to be a species that displayed ontogeny due to them mainly being observed in coastal waters (Compagno, 1984). It was not until the advancement and implementation of satellite tags by GWS biologists that a discrepancy in habitat and migration was noticed between age groups (Boustany *et al.*, 2002; Bonfil, 2005; Weng, 2007; Nasby-Lucas *et al.*, 2009; Jorgensen *et al.*, 2010). Bruce and Bradford (2012) noted that coastal waters are dominated by GWS that have a total length <3m, whilst Jorgensen (2012) reported that pelagic waters are dominated by mature adults. Both observations are supported by research conducted by Curtis *et al* (2014) and Skomal *et al* (2017). This difference in migration and habitat use has been attributed to the GWS's ontogenetic ability to raise their internal body temperature to roughly 5°C warmer than that of the surrounding water (Carey and Teal, 1969), thus enabling access to colder and potentially more rich waters (Carey *et al.*, 1982; Smith and Rhodes, 1983; Carey and Casey, 1985). Additionally, a dietary shift has been identified in GWSs, from small bony fish and coastal taxa to larger more pelagic organisms such as marine mammals, large cephalopods and other sharks (Estrada *et al.*, 2006; Smale and Cliff, 2012).

The presence of ontogeny in *C. carcharias* is therefore believed to have a large impact on their migratory patterns and habitat selection as they have differing needs dependent upon their life stage. Although ontogeny in *C. carcharias* is widely accepted, some do not believe it has a significant impact on their migration. Curtis *et*

al (2014) noted that all life stages were present in coastal waters year-round. Additionally, tagging of GWS has shown that all life stages are present in the shared off-shore foraging area in the pelagic pacific (Domeier and Nasby-Lucas, 2008). Some researchers have even put forward counterarguments, detailing that individuals <4m reside in coastal waters to avoid predation from other larger sharks (Klimley and Anderson, 1996; Goldman and Anderson, 1999).

Apart from age, there is one other major difference when comparing migration patterns of GWS's. Mature males make an annual migration coinciding with seasonal changes in SST, whereas females make a biannual migration into more pelagic environments (Anderson, 2003). Sexual segregation is almost universal across all shark species (Bres, 1993) and *C. carcharias* is no exception (Bruce *et al.*, 1996; Pardini *et al.*, 2001; Sims, Nash and Morritt, 2001; Anderson, 2003; Jorgensen *et al.*, 2010, 2012; Domeier and Nasby-Lucas, 2012; Francis *et al.*, 2012; Robbins and Booth, 2012; Milankovic *et al.*, 2021). This segregation is most clear in work by Domeier and Nasby-Lucas (2012), who showed that in the Pacific males and females only share waters for ~90 days every two years. This segregation led to the creation of many theories attempting to elucidate why, one being that females undergo separate migrations away from males in order to birth and protect their pups from cannibalism (Springer, 1967; Domeier, 2012; Domeier and Nasby-Lucas, 2012), however, this theory does not explain the segregation seen in individuals as small as 2.2m (Bruce *et al.*, 1996). Other theories such as those proposed by Robbins and Booth's (2012) hypothesize that females opt for warmer water to promote embryonic growth. Pyle *et al* (1996) also hypothesize that that oceanographic fronts can limit GWS movement.

Another factor closely examined when looking into GWS migration is bathymetry. Many satellite tagging operations fit sharks with depth profilers allowing the researcher to note time at depth of an individual. This may have been done in the hope of explaining their migration and behaviour, but it seems to have only provided more questions than answers. Table 2 summarises the recorded depths GWSs have been observed to frequent.

Table 2: Average depth bins recorded by tagged *c. carcharias* specimens across the world.

Geographical population	Depth range (m)
Australia	0-5m OR 60-100m
New Zealand (coastal)	<50m
New Zealand (oceanic)	0-1m OR 200-800m
Guadalupe (Mex)	0-10m OR 200-300m
North Atlantic	<50m OR 200-600m
South Africa	0-1m OR 500-700m

Interestingly it can be seen that *C. carcharias* is a bimodal swimming species, inhabiting either shallow or midwater depths (Bonfil, 2005; Bruce, Stevens and Malcolm, 2006; Bruce and Bradford, 2012; Domeier, Nasby-Lucas and Lam, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Skomal *et al.*, 2017).

Despite this behaviour being universally observed, the reasoning behind it and therefore how it may impact their migration is still an area of contention. Observations of this bimodal swimming pattern led Jorgensen *et al.* (2012) to hypothesise that this may be a type of Lek mating behaviour, but this fails to explain why this behaviour is seen in females and juveniles. One observation made by Goldman *et al.* (1996) is that GWS' swimming depth seems to be closely related to bathymetry - leading to the theory that *C. carcharias* may use bottom topography as a map, diving to the bottom for reference during voyages (Bruce, Stevens and Malcolm, 2006; Bruce and Bradford, 2012). Moreover, a current theory gaining more traction is that of geo-electromagnetic detection, in which the sharks explore the vertical water column looking for electromagnetic anomalies and use these as a sort of mapping system utilising reference points (Klimley *et al.*, 2002; Keller *et al.*, 2021).

Finally, one of the most important and potentially influential factors in *C. carcharias*' migration dictating the convergence and divergence of this sexually segregated taxa is mating (Sims, Nash and Morritt, 2001; Domeier and Nasby-Lucas, 2012; Jorgensen *et al.*, 2012). Yet there has been no advancement in this field since Francis' (1996) report which outlined the current gap in knowledge regarding: where they mate, how they mate, the associated behaviour with mating and where they go to birth.

Aims and Objectives

Despite the intricacies of GWS migration not yet being fully understood, data collected from tagged individuals has allowed us in part to see what oceanographic parameters and ecological conditions they frequent. These conditions are near identical to those of British waters, sharing similar temperature, salinity, and depth ranges, and possessing a wealth of prey items. Adding to the confusion is the fact that there have been over 100 sightings of GWS's in British waters and *C. carcharias* specimens have been caught as close as the Bay of Biscay as seen in Figure 4. Therefore, the main aim of this investigatory report was to; Explore the habitat suitability of British waters for *C. carcharias* in an effort to identify a reason for their absence.

This aim was met by achieving a collection of objectives that worked in conjunction with one another. These were:

1. Map the oceanographic and ecological conditions of known GWS habitats.
2. Create a species distribution model of tagged GWS to examine the accompanying oceanography of their migratory routes.
3. Identify and quantify key influencing environmental factors in GWS habitat selection
4. Cross reference the models produced with the scientific literature to add ecological/ biological reasoning behind their absence in British waters.

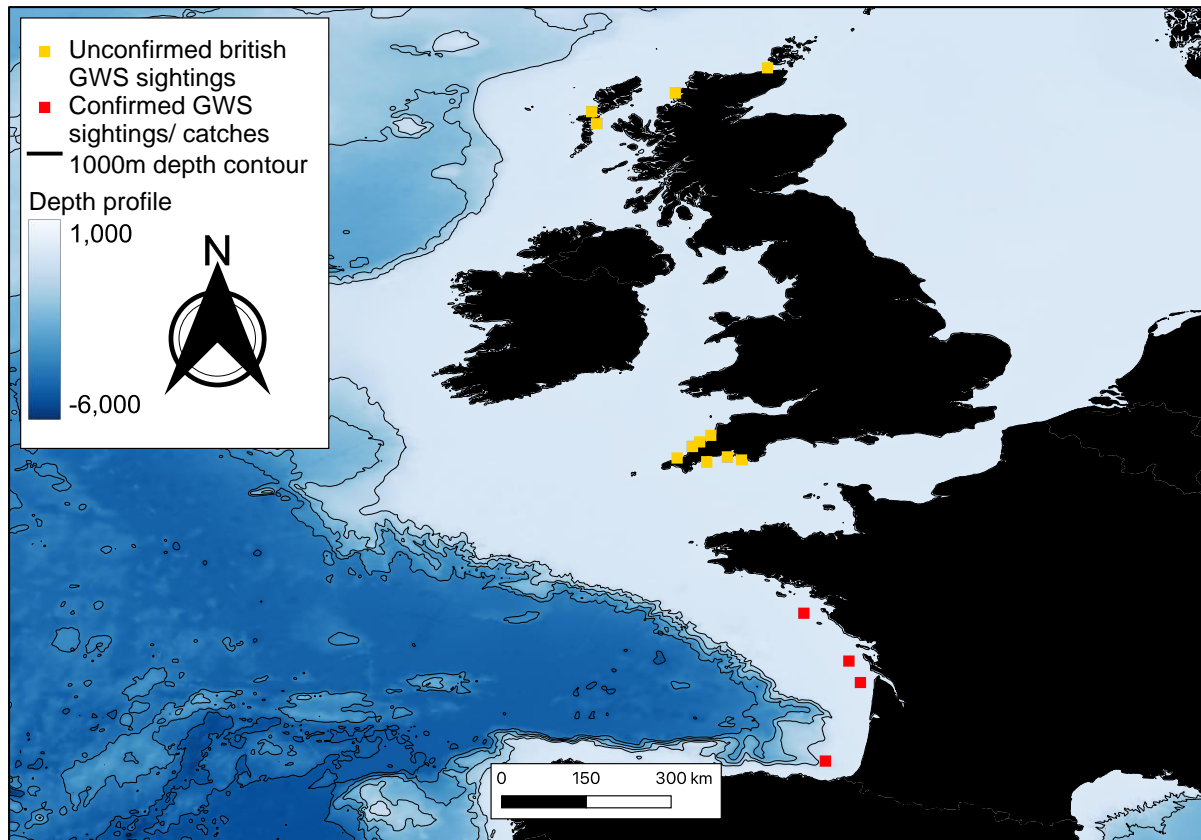


Figure 4: Map of western Europe showing unconfirmed GWS sightings (Yellow) and confirmed GWS sightings (Red). Map produced by author on QGIS.v3.18 using data from Noaa.gov.ETOPO1 and Richard Peirce's 2016 book "UK's Great White Shark Enigma".

Methods

For this study, species distribution models were created for *C. carcharias* by means of Boosted Regression Trees (Hereafter abbreviated to BRT). Models were developed using presence data from tagged sharks, pseudo-absence data and environmental variables that are tied to habitat selection. (Hernandez *et al.*, 2006; Elith, Leathwick and Hastie, 2008; Peterson and Nakazawa, 2008). Variables known to affect the occurrence of their prey items were also included (Dambach and Rödder, 2011), these are:

- Sea Surface Temperature (°C)
- Depth (m)
- Chlorophyll (mg^{-3})
- Sex

These variables in union with migration data, presence/ absence data, georeferencing and GIS mapping were used to create a species distribution model.

GWS Migration Tracking

To create an accurate model using presence data (Hernandez *et al.*, 2006; Wisz *et al.*, 2008) four mature GWSs named "George", "Jefferson", "Lydia" and "Nukumi" were chosen to be geo-referenced for this study. The two females (Lydia and

Nukumi) were chosen especially as they have crossed the mid-Atlantic ridge and are the closest venturing GWS's to British waters from the north Atlantic population. All steps taken within this sub-section have been summarised In Figure 5.

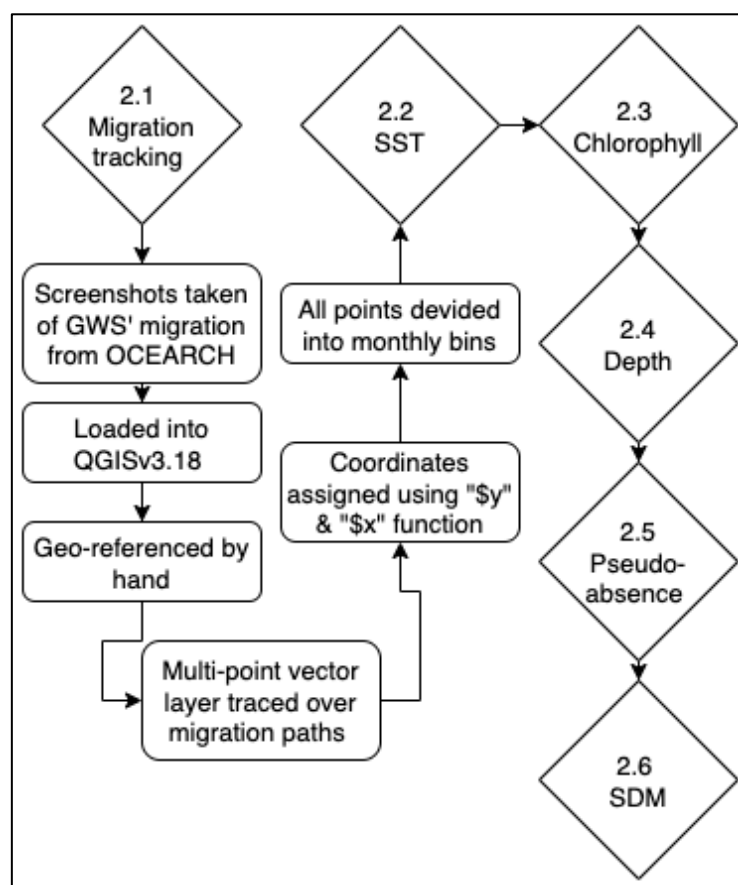


Figure 5: Flow chart summarising steps taken within the 'Migration tracking' methodology subsection.

Screen-prints were taken of the GWS's migration and loaded into QGIS.v3.18 using the georeferencing tool. Once loaded in, a multipoint vector layer was created over each shark's migratory path, creating an attribute table for each individual. (Geo-referencing is not a 100% accurate method for transcribing maps and therefore should be noted that point accuracy may vary from 1-5km; to mitigate this, all SST data were collected in 9km bins.) Once George, Jefferson, Lydia and Nukumi's migration points were plotted, coordinates were assigned to each point. They were then divided into 61 monthly bins spanning the dataset.

Sea Surface Temperature

SST, as previously stated, is regarded as a key environmental variable determining GWS habitation and migration (Carey *et al.*, 1982; Carey and Casey, 1985; Cliff, Dudley and Davis, 1989; Bruce *et al.*, 1996; Goldman *et al.*, 1996; Long *et al.*, 1996; Pyle *et al.*, 1996; Anderson, 2003; Bruce, Stevens and Malcolm, 2006; Domeier and Nasby-Lucas, 2008, 2012; Nasby-Lucas *et al.*, 2009; Bonfil *et al.*, 2010; Bruce and Bradford, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Skomal *et al.*, 2017; Milankovic *et al.*, 2021), therefore it is one of the primary variables included in this

investigation. Despite this SST is not always indicative of the temperature at which the GWS may occupy.

SST was obtained from Giovanni.gsfc.nasa.gov, the data ranged from 2013-2021, totalling 61 months; see Table 3. All SST data was collected from the MODIS-Aqua satellite, sampling at 4 microns at night in 9km bins every 8 days. 9km bins were chosen to reduce data handling size and to ensure data allocation accuracy when assigning values to the migration paths. SST was collected at night using a 4-micron wavelength, these settings were used to reduce water vapour interference and to ensure data quality. All data was downloaded in GeoTIFF format for input into GIS software.

Table 3: Dates when remotely sensed SST and chlorophyll data were extracted.

Year	Month
2013	January, April, May, June, July, August, September, October, November, December
2014	January, February, March, April, May, June, July, September, October, November, December
2015	January, February, March
2016	May, June, October, November, December
2017	January, February, March, April, August
2018	January, February, March, April, June, July, August, September, October, November, December
2019	January, March, April, August, September, November
2020	January, February, March, April, October, November, December
2021	January, February, March, April, October

Chlorophyll-a

Chlorophyll-a is a green pigment found within plant cells and can be used as a good proxy for phytoplankton abundance because it is the most dominant photosynthetic pigment. This measurable abundance can be used as trophic gauge (Anzecc, 2000; Boyer *et al.*, 2009) and was selected as a variable to indicate potential prey items for the GWSs (Murray and Orphanides, 2013; Dodge *et al.*, 2014; Stepanuk *et al.*, 2018; Kohler and Turner, 2020; Latour and Gartland, 2020)

All Chlorophyll data utilised in this report was obtained from Giovanni.gsfc.nasa.gov via remote sensing from MODIS-Aqua satellite sampling every 8 days in 4km bins. 8-day resolution were chosen as it allowed for a more accurate mean when compiling a monthly average. Despite 9km bins being more desirable as they were used for SST, 4km bins were the only available option. Data were exported as GeoTIFF files for all months detailed in table 3, then overlaid onto QGIS.v3.18 for manipulation.

Depth

The third variable in this investigation was depth. Depth is also recognised as being important in GWS migration (Goldman *et al.*, 1996; Boustany *et al.*, 2002; Bonfil, 2005; Bruce, Stevens and Malcolm, 2006; Bruce and Bradford, 2012; Domeier, Nasby-Lucas and Lam, 2012; Francis *et al.*, 2012). Depth data was extracted from NOAA's ETOPO1 (bedrock) database. A polygon was created around the north Atlantic and the study domain (Figure 1). These polygons were then extracted as GeoTIFFs.

Pseudo-absence data

Elith *et al.*'s (2008) method of using BRTs to explore the relationship between environmental variables and their impact upon species habitat selection requires presence and absence data. Phillips and Dudík (2008) recommend the use of pseudo-absence data as a substitute due to absence data being difficult to obtain, therefore this was used to train the machine learning what environmental parameters GWSs are not present in. To do this, polygon vector layers were created around areas in the north Atlantic where the tracked sharks were never present throughout their migrations. 100-250 points were then generated within these polygons using a randomiser tool within QGIS.v3.18. One of the 61 months of SST and Chlorophyll data were selected and assigned to these points, thus producing 100-250 data points populated with: date, SST, Chlorophyll, and depth values where GWS were not present. This process was repeated until 700 Pseudo-absence values were produced.

Species distribution modelling & Boosted regression trees

Species distribution modelling through BRTs was used in this investigatory report as this method has been widely utilised in predicting the distribution of migratory species for years (Carey *et al.*, 1982; Buckland and Elston, 1993; Elith, Leathwick and Hastie, 2008). BRTs identify the non-linear relationship between a response variable and group of weak predictor variables, in this case, the variables being environmental conditions identified such as SST and Chlorophyll, and the GWS's habitat choice being the response variable. All steps in this sub-section have been summarised in Figure 6.

To produce a working model, code from Elith *et al.*'s (2008) paper was used as a foundation. Firstly, the data was imported into RStudio_2021.09.2 and randomised as it was found that this improved model accuracy. Once imported, the data was split 70-30 to allow for independent validation of the final model. Model learning rate and tree complexity values were varied (Table 4) to find the model with best predictive power.

Table 4: Tabulation of all outputs created when altering the Learning rate and Tree complexity within the first iteration of modelling. “se”= Standard error.

		1 st Iteration		
Estimated Cross Validation Deviance		Learning Rate		
		0.05	0.01	0.005
Tree Complexity	1	0.568; se = 0.018	0.577; se = 0.012	0.591; se = 0.019
	2	0.487; se = 0.014	0.497; se = 0.03	0.492; se = 0.025
	3	0.469; se = 0.027	0.472; se = 0.021	0.469; se = 0.019
	4	0.454; se = 0.017	0.459; se = 0.026	0.457; se = 0.019
	5	0.455; se = 0.012	0.459; se = 0.03	0.449; se = 0.021

Iterations 2 – 8 were run with a tree complexity of 4 & 5 as these were found to produce the most accurate models, then 8-15 were run with a tree complexity of 5 as it had become evident that this was the best setting for the model. Additionally, a learning rate of 0.005 was found to reliably produce the lowest cross validation deviance. A `gbm.summery` function (Elith, Leathwick and Hastie, 2008) was used to show how much each variable affected habitat selction (Figure 11). The final model was named ‘*Shark.fit.Lr.0.005.Tc.5*’. Model ‘*Shark.fit.Lr.0.005.Tc.5*’ was then run 100 times with random subsampling from the full dataset to generate the mean and stand deviation of the shark response functions to each enviromental variable. The new file containing the 100 repeats was then used to produce 3 plots each displaying a variables’ range and influence at their respective differing values (Figure 12).

Next, SST & Chlorophyll NetCDF files from 2010-2020 were downloaded in seasonal bins. A depth profile of the study area was also extracted from Noaa.gov.ETOPO1 and overlaid onto QGIS.v3.18 - automatically assigning depth values appropriate coordinates. All files were then imported into MATLAB_R2019a where SST and Chlorophyll value were assigned coordinates. These new values were amalgamated into a CSV containing SST, Chlorophyll and depth values for every data point within the study area; two variations of these lists were created containing a sex column, one male, one female. This process was repeated for all 4 seasons (Oberhauser and Peterson, 2003) untill a total of 8 amalgamated files were produced. These new amalgamated files were imported into RStudio_2021.09.2 and the ‘*Shark.fit.Lr.0.005.Tc.5*’ prediction model was run to predict GWS presence-absence in British waters. This was repeated with the 8 amalgamation datasets to produce prediction txt files. These prediction files were exported from RStudio_2021.09.2 into MATLAB_R2019a and reshaped into a grid format.

To interrogate the data, a function called `gbm.perspec` (Elith, Leathwick and Hastie, 2008) was used. Plotting the interaction of 2 variables and visualising their effect on the model output, these can be seen in Figure 16.

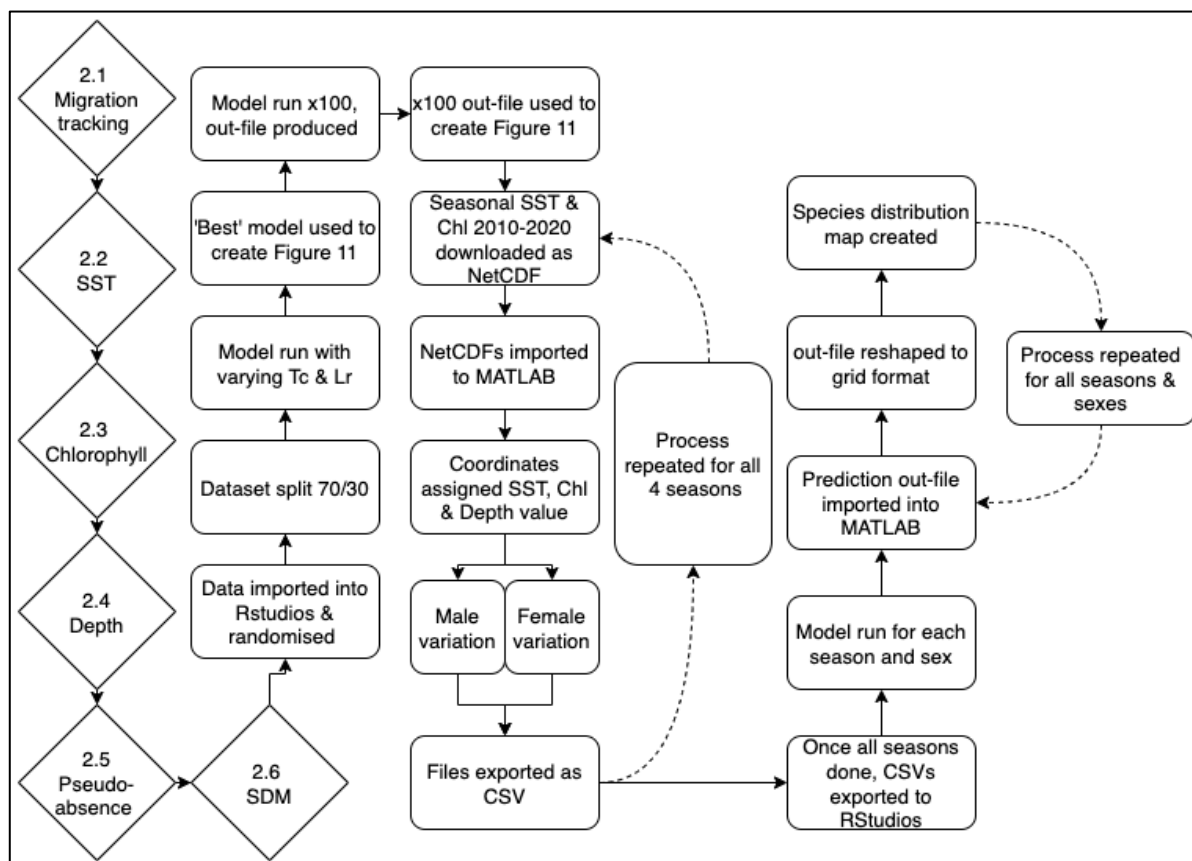


Figure 6: Flow chart summarising the steps taken during the 'SDM & BRT' methodology subsection.

Results

Migration mapping

Figure 5 to 8 illustrate the migratory path of GWSs George, Jefferson, Lydia and Nukumi. Every time the shark broke <5m depth a transmission of the coordinates was relayed (as highlighted by coloured circles). Furthermore, their paths have been interpolated from each point to the next, creating an inferred migratory route.

Figure 7 shows the yearlong migration of a female GWS; Nukumi. This migration is what would be expected from a mature female; spending time in shallow waters but eventually venturing into a more deep-water pelagic environment (Bres, 1993; Bruce *et al.*, 1996; Ferreira and Ferreira, 1996; Sims, Nash and Morritt, 2001; Domeier, 2012; Domeier and Nasby-Lucas, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Robbins and Booth, 2012; Milankovic *et al.*, 2021).

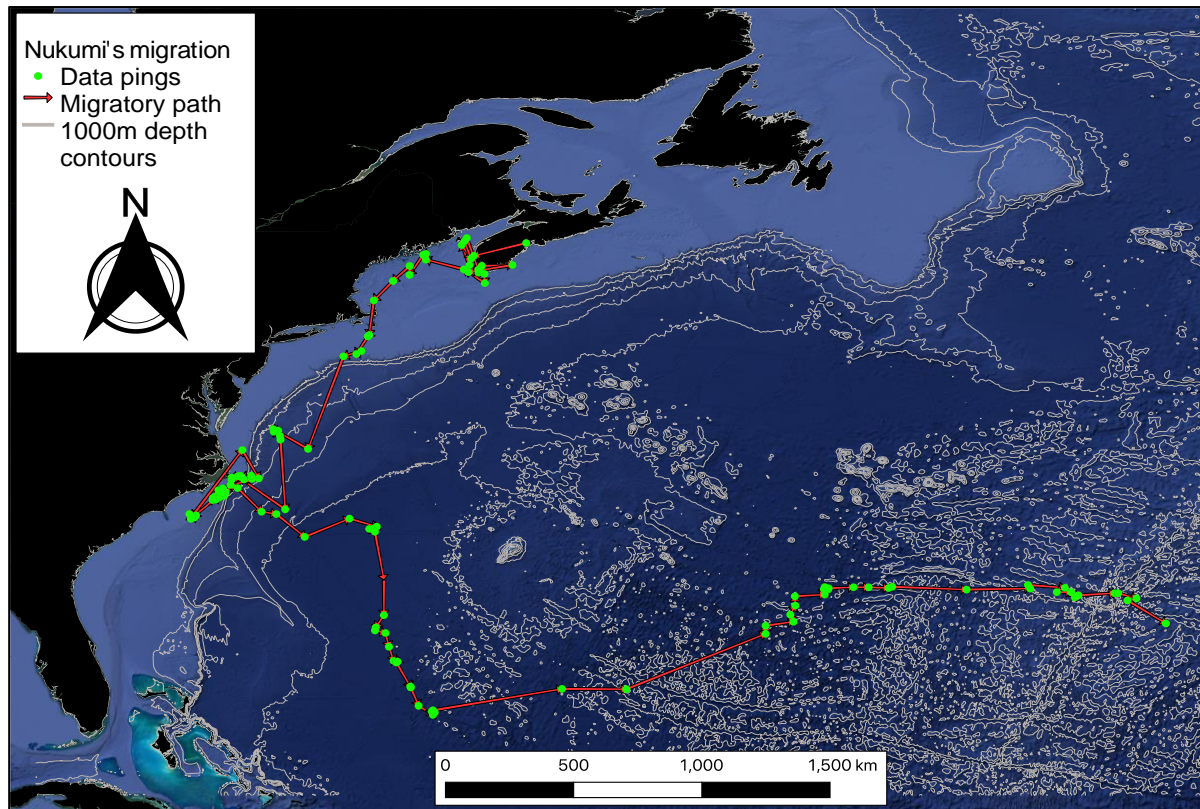


Figure 7: Migratory route of female GWS “Nukumi” from 2020/10 – 2021/10 with 1000m contour lines. Data sourced from OCEARCH and Noaa.gov.ETOPO1.

Figure 8 displays the migration of a mature male; George, spanning roughly 2 years. This migration is what would be expected from a male GWS, spending the majority of their time in coastal waters (Bres, 1993; Bruce *et al.*, 1996; Ferreira and Ferreira, 1996; Sims, Nash and Morritt, 2001; Domeier, 2012; Domeier and Nasby-Lucas, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Robbins and Booth, 2012; Milankovic *et al.*, 2021), although, it can also be noted due to the sparsity of pings, that the individual spent a majority of their time at depths >5m.

Figure 9, is a stereotypical migration for a mature male (Bres, 1993; Bruce *et al.*, 1996; Ferreira and Ferreira, 1996; Sims, Nash and Morritt, 2001; Domeier, 2012; Domeier and Nasby-Lucas, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Robbins and Booth, 2012; Milankovic *et al.*, 2021) staying in coastal waters following a latitudinal gradient with the changing seasons. Similar to Figure 6, it also infers that a large amount of time was spent at depths >5 meters.

The intricate 5-year migration of Lydia; a mature female GWS, can be seen in Figure 10. This individual spent a large amount of time in the open oceans and near coastal shelves; a behaviour well documented within existing literature. Furthermore, Lydia also frequented <5m depth much more than the male GWSs.

Species distribution modelling

Figure 11 shows the influence of each variable on *C. carcharias* habitat preference as a percentage. It can be seen that all variables are nearly equal in influence, although, SST seems to be the most influential.

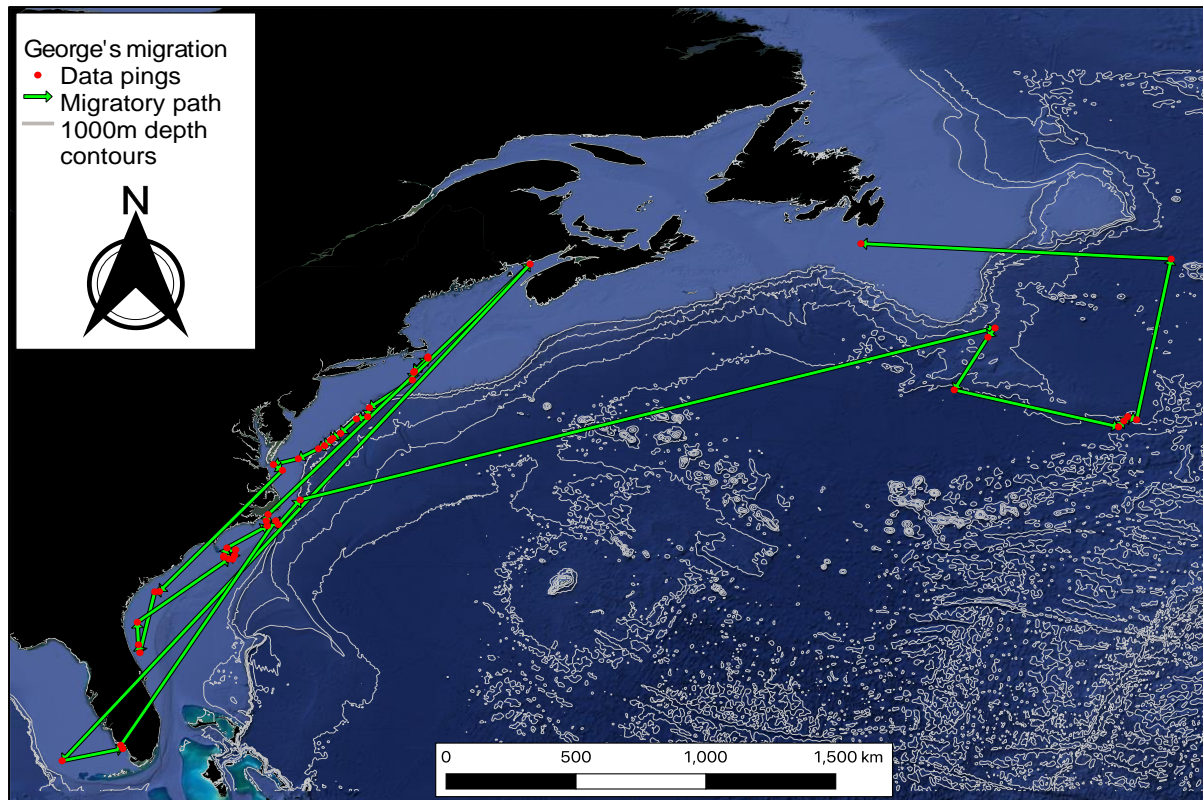


Figure 9: Migratory route of male GWS "George" from 2016/10 – 2018/08 with 1000m contour lines. Data sourced from OCEARCH and Noaa.gov.ETOPO1.

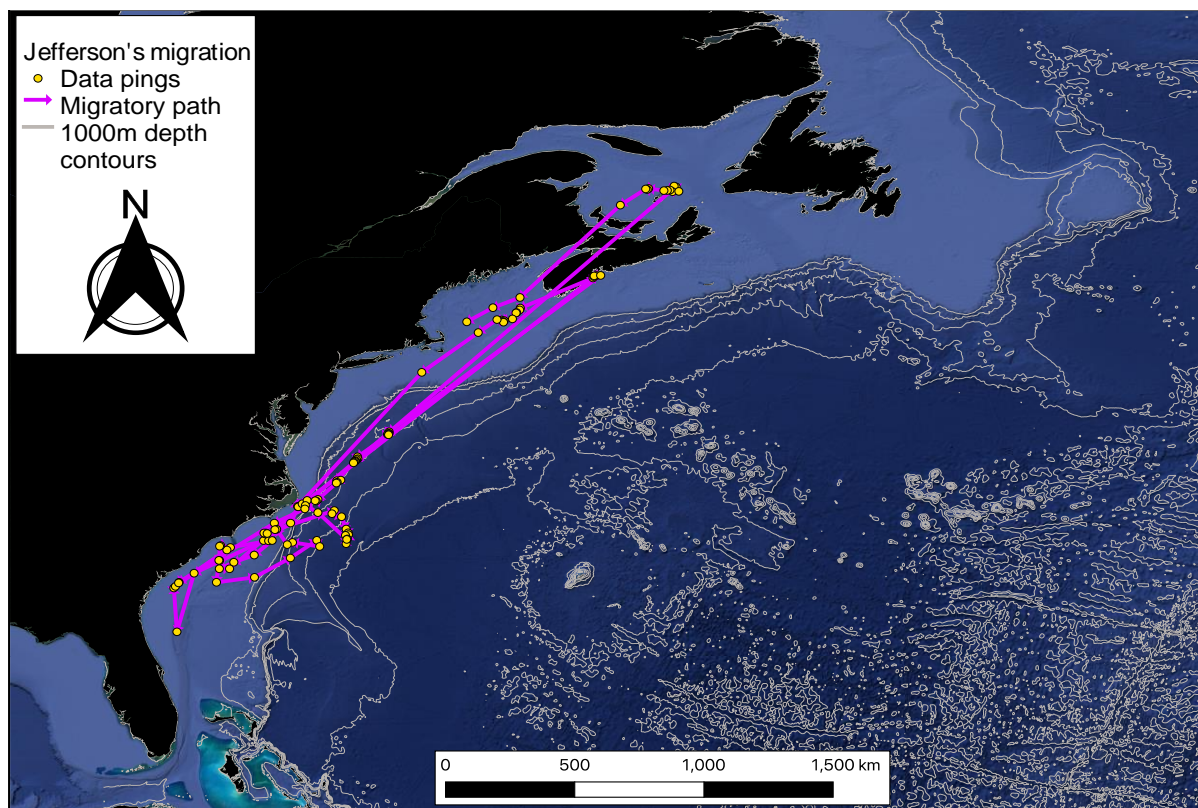


Figure 8: Migratory route of male GWS "Jefferson" from 2018/09 – 2020/11 with 1000m contour lines. Data sourced from OCEARCH and Noaa.gov.ETOPO1.

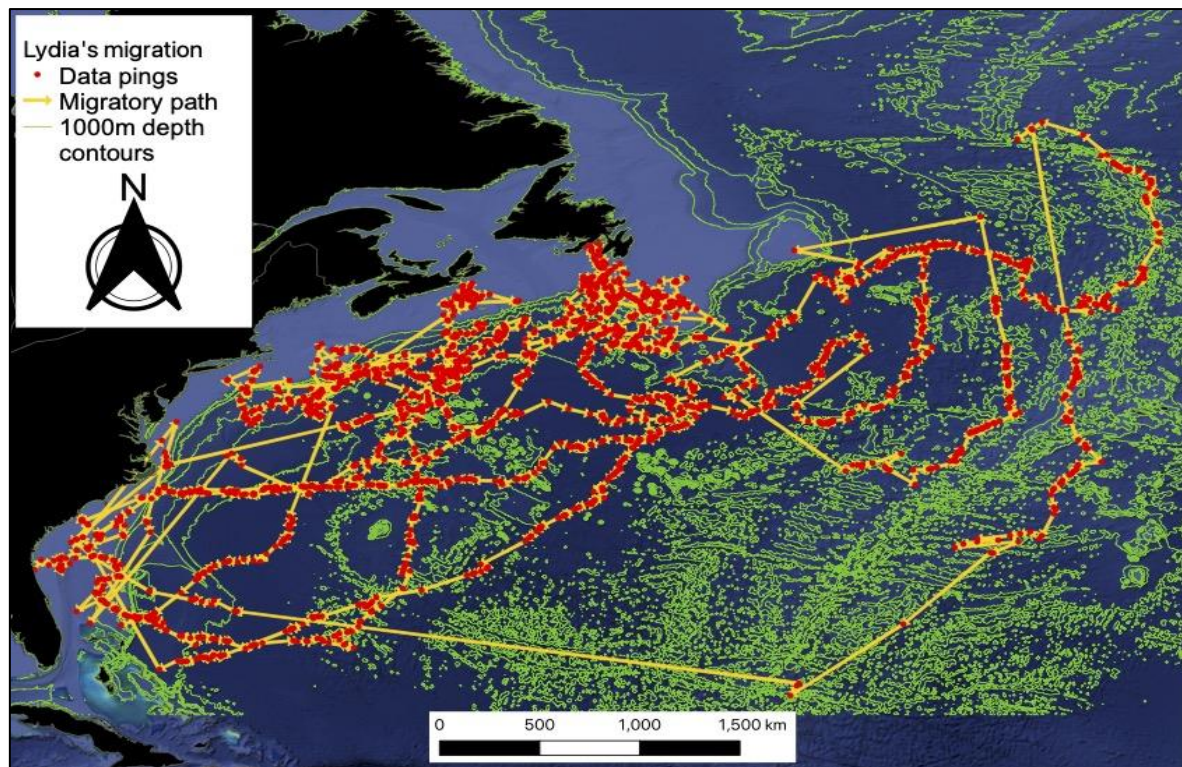


Figure 10: Migratory route of female GWS “Lydia” from 2013/03 – 2018/06 with 1000m contour lines. Data sourced from OCEARCH and NOAA.gov.ETOPO1

Figure 12 is a breakdown displaying habitat suitability on the Y-axis and the variables respective data range on the X-axis, displaying the differing suitability dependant on the environmental parameter. Sex was excluded as there is no measurable gradient. In plot A it can be noted that although there is an average increase in predictability with temperature rise, there are fluctuations. A drop in habitat suitability can be seen between $\sim 13.5^{\circ}\text{C}$ and $\sim 18^{\circ}\text{C}$ but then a sudden climb, this pattern is then repeated between $\sim 24^{\circ}\text{C}$ and 25.5°C until 26°C where it levels out. Plot B displays a distinct preference for waters where the Chlorophyll concentrations are $>0.5\text{mg}^{\text{m}^{-3}}$, Plot C on the other hand is more heterogeneous. In this plot, a positive correlation between shallowing waters and habitat preference can be seen. There are fluctuations, between 3100m-1800m depth. Despite this, there is a clear preference for waters shallower than 1,600m.

Figure 13 depicts the probability of a male and female GWS inhabiting British waters in the winter. A discrepancy between the two sexes' suitability to the research area can be seen, with females showing prediction values >0.80 for the whole area, as opposed to the male's range of >0.30 .

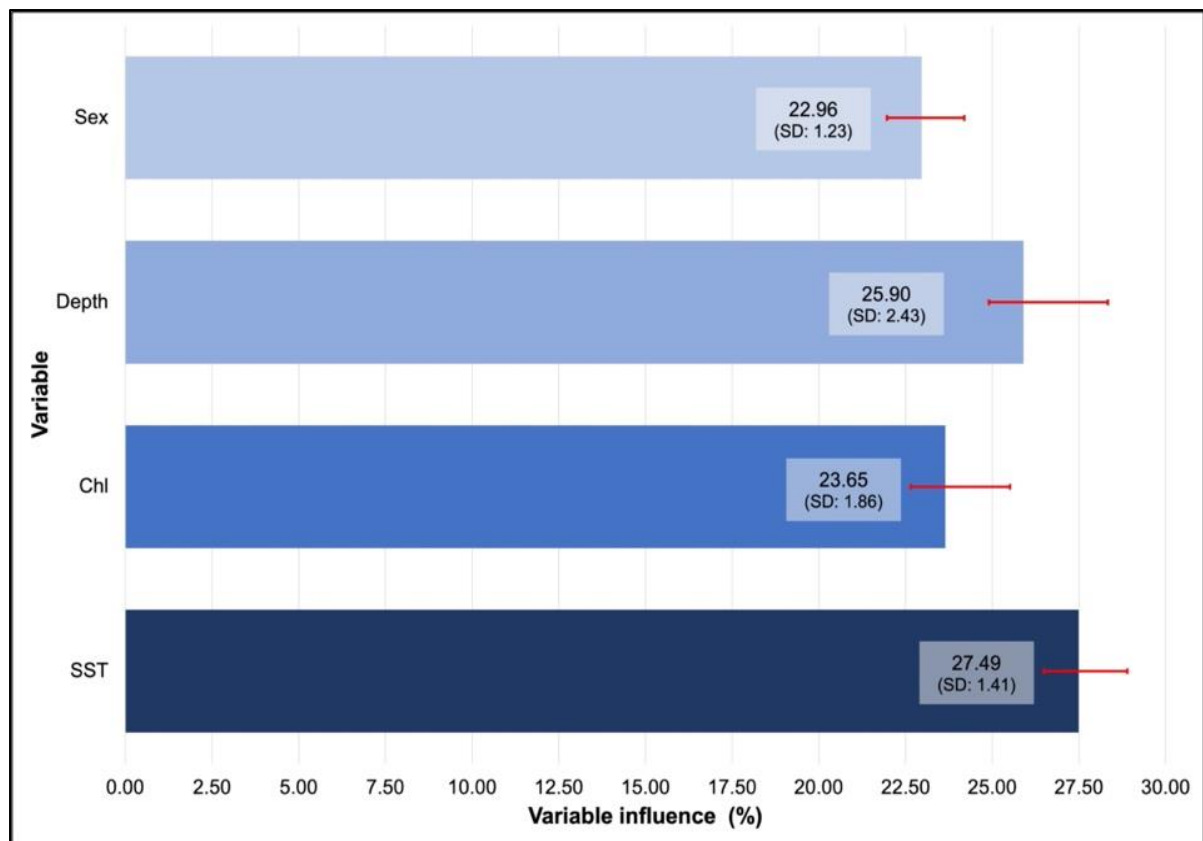


Figure 11: Variables influence on GWS habitat selection as a percentage with their respective standard deviations.

A plot of the springtime habitat suitability was not included in this report as the entire study area showed a likelihood of >0.95 for both sexes showing no deviation. The likelihood of finding *C. carcharias* in British waters during Summer can be seen in Figure 14. Like the last two Figures, a vast majority of the study area exhibits >0.90 habitat suitability. Lower predictability (~0.60) seems to be situated to the west and southwest, but there is also a small area with values of ~0.70 found between latitudes 55-59 and longitudes 0-2.

The Autumnal season displayed in Figure 15 has a more heterogenous habitat suitability for both sexes. Once again, the southwest portion of the study area seems to exhibit a lower habitat suitability compared to the rest of the waters. Furthermore, this season displayed the widest range in suitability with values as low as ~0.25.

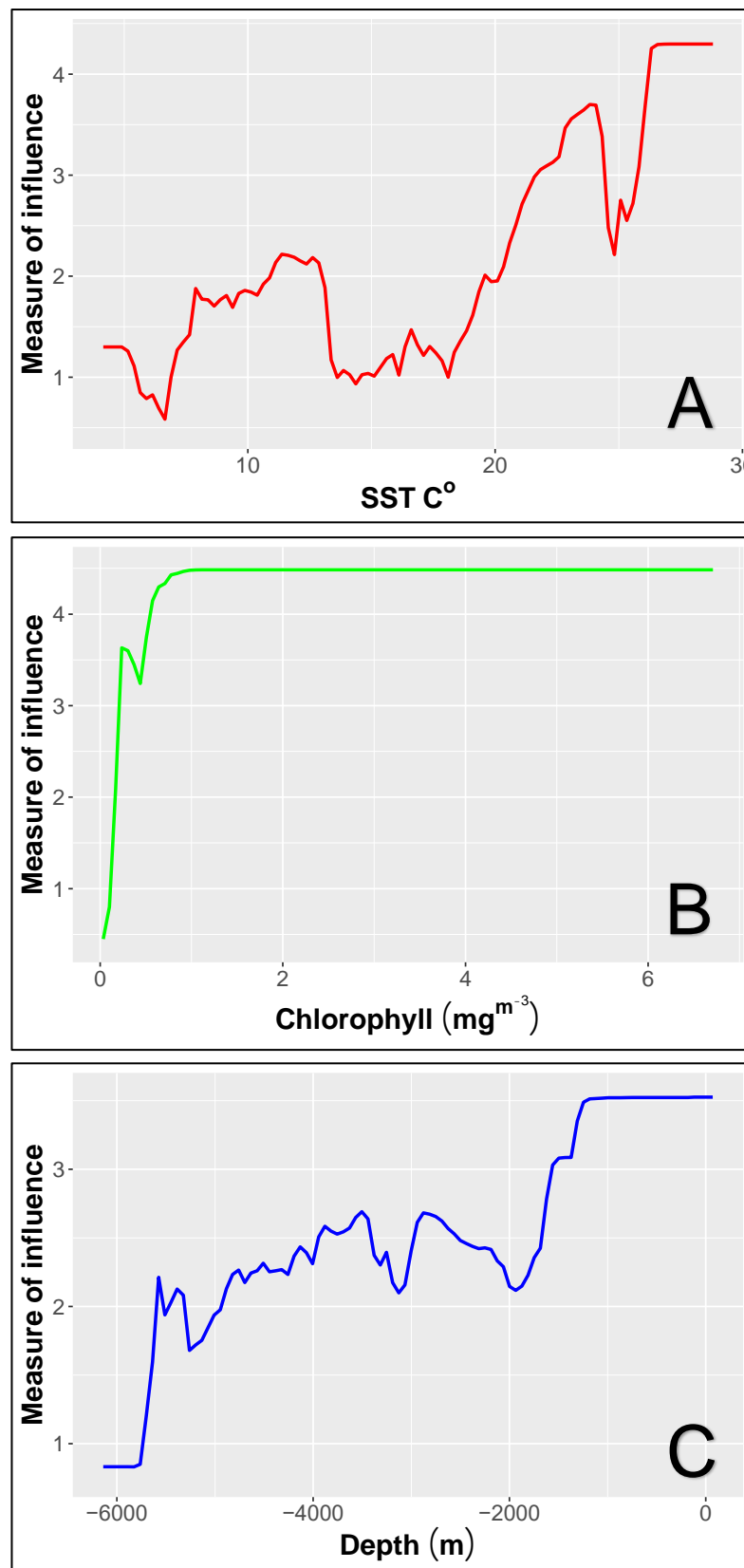


Figure 12: The influence of each measurable variable along their respective gradients. (A) SST in red measured in Celsius, (B) Chlorophyll in green measured in concentration per milligram and (C) Depth in blue measured in meters. Each parameters standard errors are included.

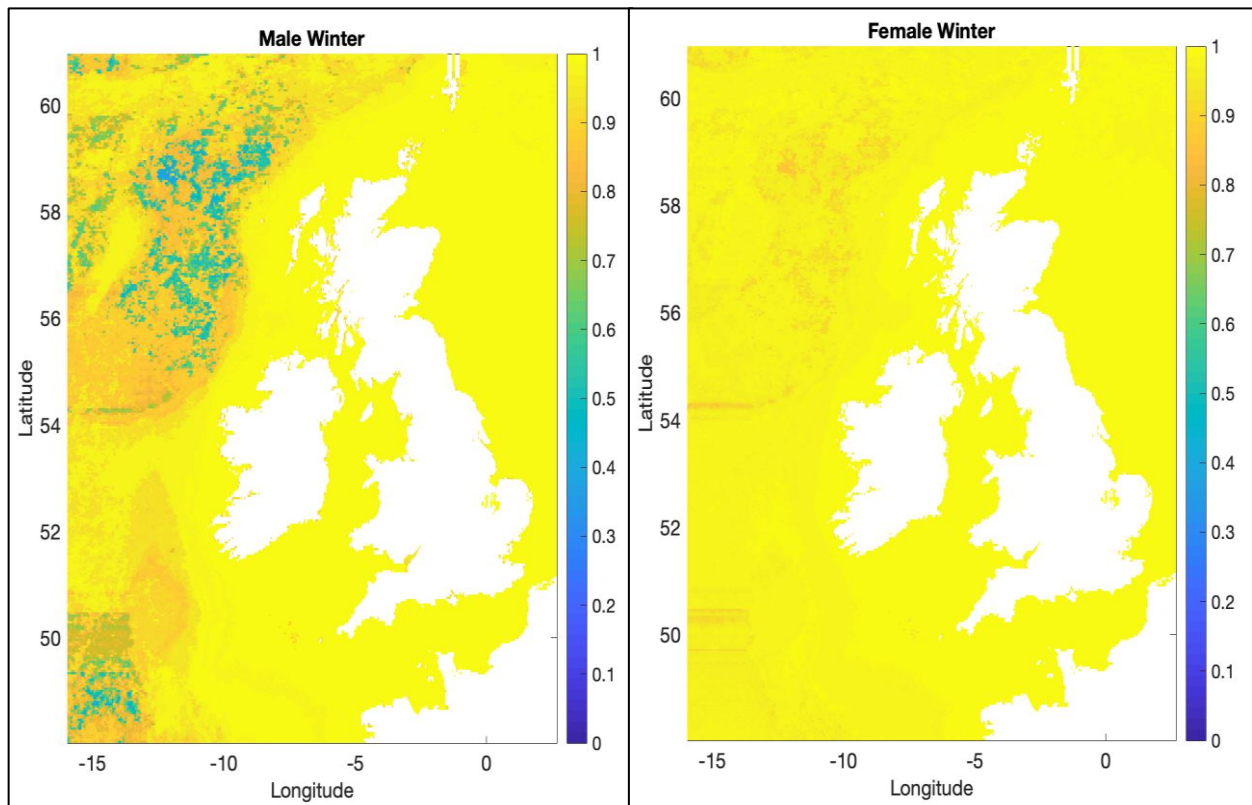


Figure 13: Species distribution map displaying the probability of a Male or Female GWs inhabiting British waters during Winter.

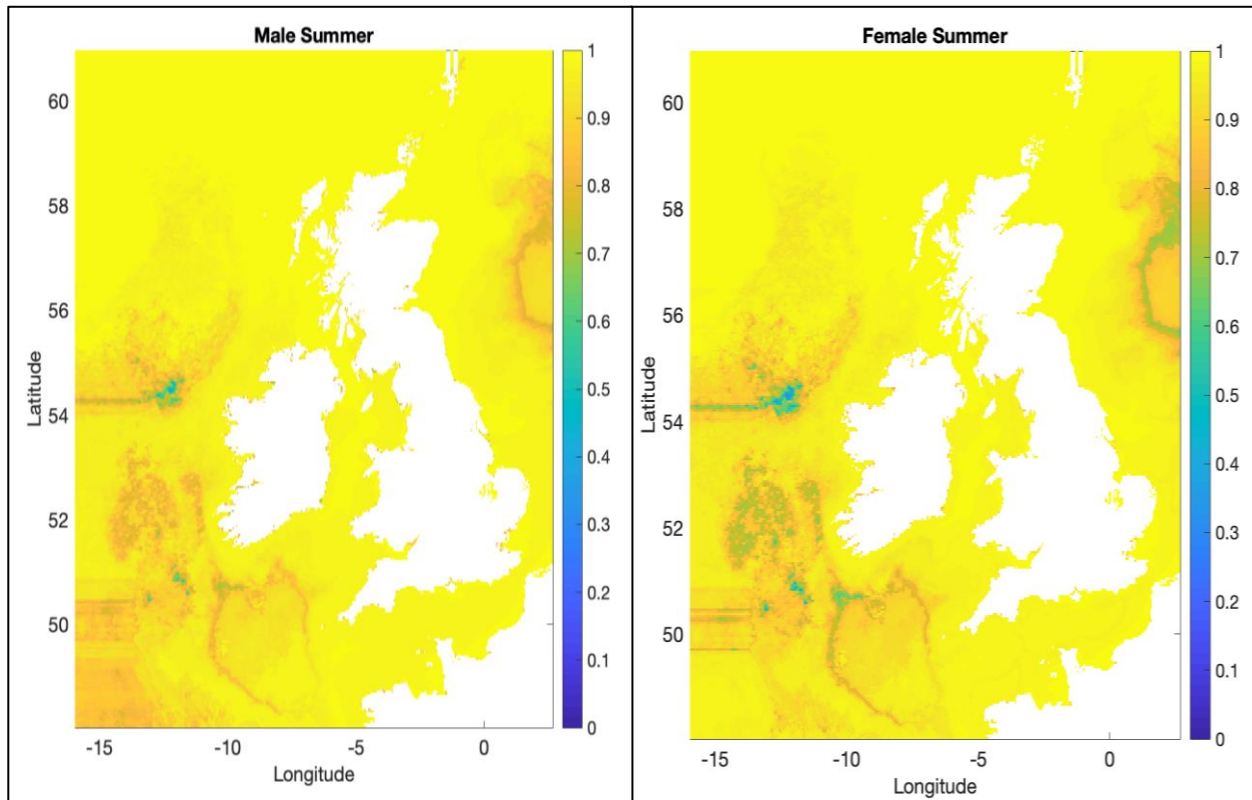


Figure 14: Species distribution map displaying the probability of a Male or Female GWs inhabiting British waters during Summer.

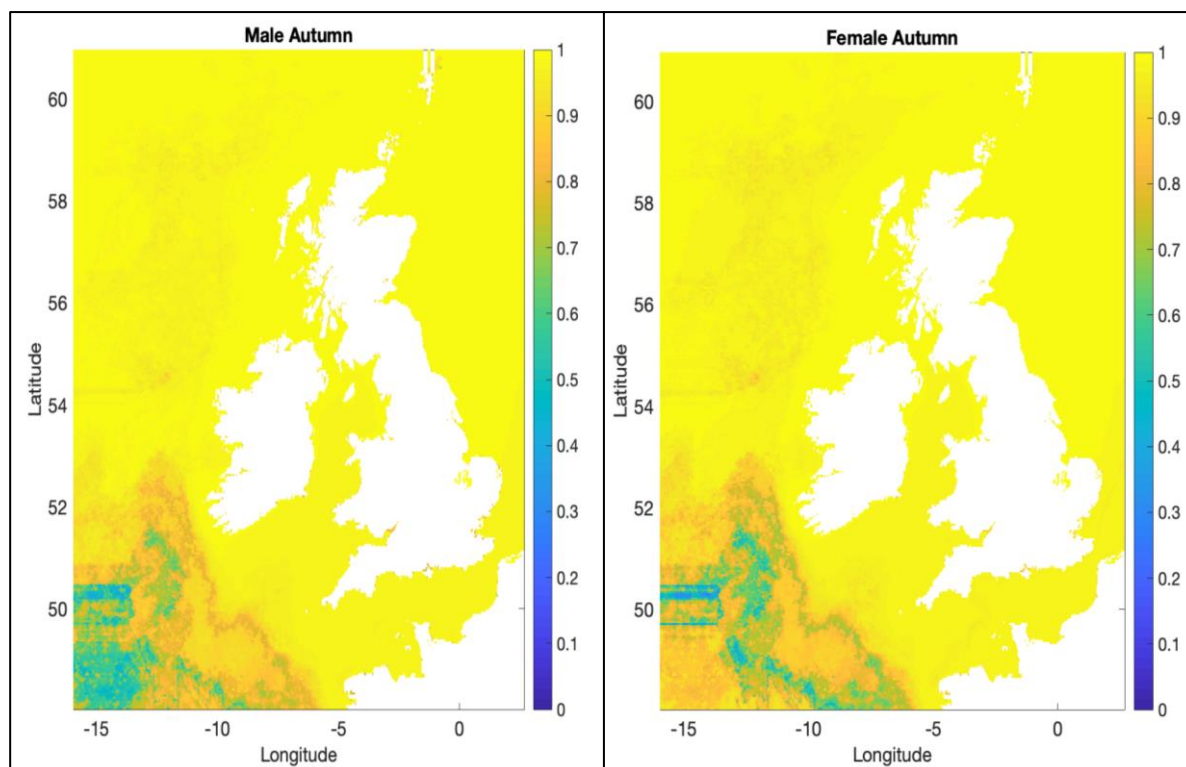


Figure 15: Species distribution map displaying the probability of a Male or Female GWSs inhabiting British waters during Autumn.

Figure 16 shows the interaction between (A) SST and Chlorophyll, (B) SST and depth, (C & D) Chlorophyll and depth, and how each parameter effects the habitat suitability. Plots A and D have had their Chlorophyll ranges capped between 0 - 1 as this is where a majority of the variation occurs values above 1 have a near homogenous effect on habitat suitability as seen in Figure 10b. Plot A exhibits a higher habitat suitability where Chlorophyll concentrations are $>0.2\text{mg}^{-3}$, except for a small drop near $\sim 0.4\text{mg}^{-3}$. This coincides with rising SST on average increasing the predictability, except between $15 - 20^{\circ}\text{C}$, where there is a drop in likelihood of GWS inhabitancy. Plot B displays a preference for warmer shallower waters with very little predictability at depths of $>2000\text{m}$ with an SST of $>12^{\circ}\text{C}$. Furthermore, a decline in likelihood can be noted in shallow waters where the SST is between $20^{\circ}\text{C} - 15^{\circ}\text{C}$. Plots C and D both display habitat suitability in regard to Chlorophyll and depth. Plot C shows the full range of Chlorophyll concentrations recorded in the data set, whereas plot D zooms to $0-1\text{mg}^{-3}$; showing how much the predictability varies between this small range.

Habitat suitability where Chlorophyll values are $<0.2\text{mg}^{-3}$ is very low across all depths. Values greater than this display an increasing predictability with depth but Chlorophyll then trails off again once $>0.8\text{mg}^{-3}$. Plot C shows that this is only a temporary drop and that likelihood quickly recovers from this dip. Interestingly a noticeable drop in suitability is displayed between depth values of $\sim 1100 - 1500\text{m}$ depth in both plots B and D.

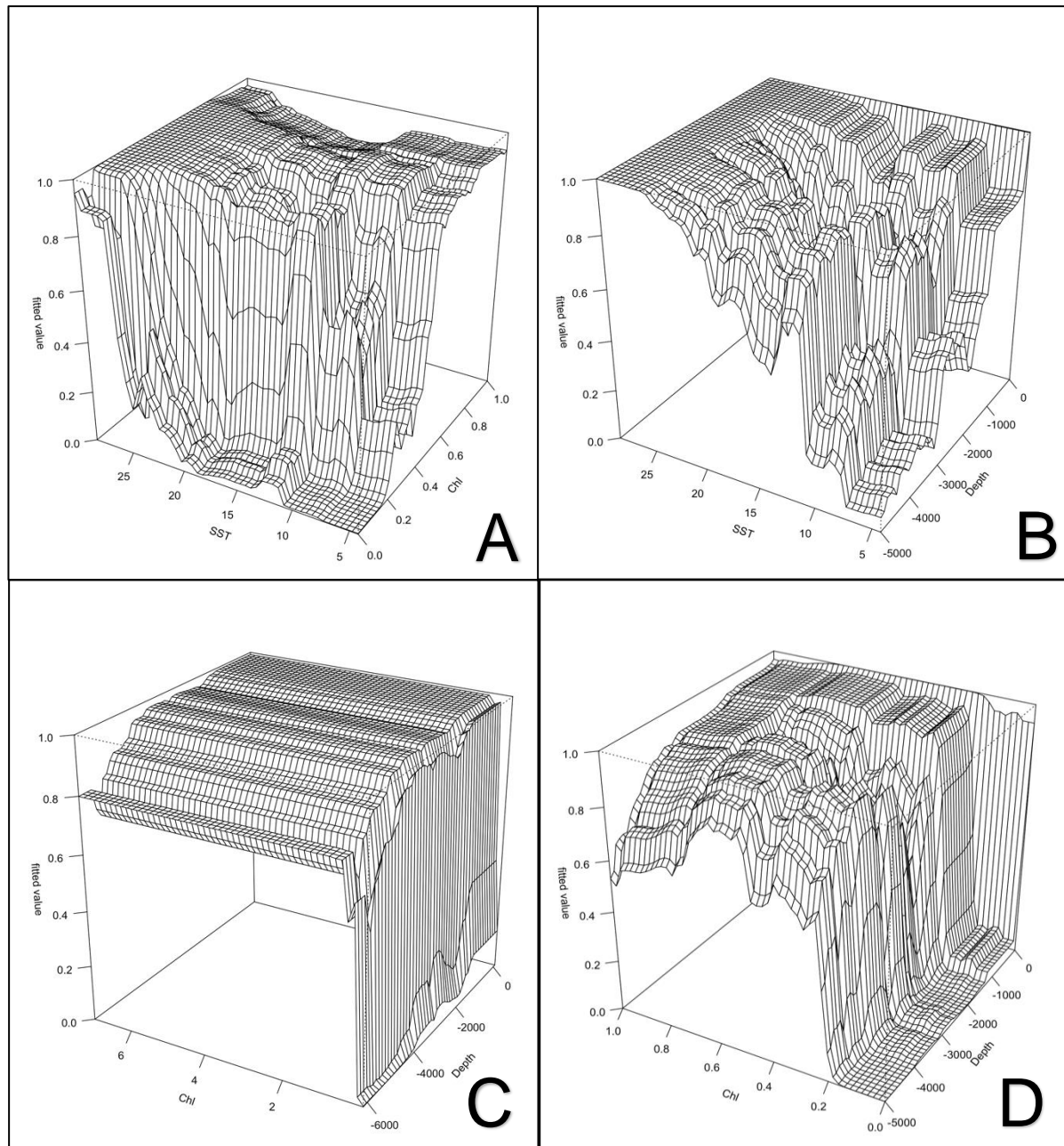


Figure 16: Three-dimensional plot showing the interactions between (A) SST and Chlorophyll concentrations between 0 – 1mg-3, (B) SST and Depth, (C) Chlorophyll and Depth, (D) Chlorophyll concentrations between 0 – 1mg-3 and Depth and their respective effect on habitat suitability. Figure created in RStudio_2021.09.2 using data produced in section 2.7.

Discussion

Whilst many reports have tracked the migration of this species; making records of the oceanography they encounter (Sims, Nash and Morritt, 2001; Boustany *et al.*, 2002; Drake, Drake and Johnson, 2005; Bruce, Stevens and Malcolm, 2006; Jorgensen *et al.*, 2010; Curtis *et al.*, 2014; Howey *et al.*, 2016; Skomal *et al.*, 2017; Shaw *et al.*, 2021) and others have employed the use of regression trees to infer populations status (McPherson and Myers, 2009), this report is the first to look into

the absence of the GWS in British waters. Furthermore, although Dambach and Rödder (2011) produced an SDM for the GWS globally, this is the first report focusing on their migration across multiple years and producing differing SDM for each season. Many steps were taken in an attempt to answer the proposed question, producing a wide range of results. Whilst some results enforced known GWS science, others questioned the literature and produced findings unmentioned in the literature up until this point.

Upon overlaying the migration of GWSs' George, Jefferson, Lydia and Nukumi onto a map of the northwest Atlantic outfitted with 1000m depth contours, it was seen that these sharks were undertaking stereotypical migrations in regard to the literature. As previously mentioned, *C. carcharias* is a sexually segregated species (Bres, 1993; Bruce *et al.*, 1996; Ferreira and Ferreira, 1996; Sims, Nash and Morritt, 2001; Domeier, 2012; Domeier and Nasby-Lucas, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Robbins and Booth, 2012; Milankovic *et al.*, 2021), with males displaying a preference for coastal waters and females more pelagic environments. Figures 6-10 display all the data pings emitted from the shark tags, these tags only relayed their location when the shark was in <5m of water, meaning when the shark was below this depth, no positioning data was recorded/ received. *C. carcharias* is a bimodal swimming species, spending vast amounts of time at depth (Goldman *et al.*, 1996; Bonfil, 2005; Bruce, Stevens and Malcolm, 2006; Bruce and Bradford, 2012; Domeier, Nasby-Lucas and Lam, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012). The female shark's migration (Figure 7 & 10) imply a majority of time spent in shallow water due to the frequency of pings - a higher frequency translates to a more accurately mapped migration. The male's migration (Figures 8 & 9) on the other hand, is much more infrequent, with Jefferson not emitting a single ping for over a year, proceeded by a flurry of shallow water activity. Likewise, George's pings seem to follow no observable pattern, emitting at one point, disappearing and then popping up more than 3000km away. Despite this lack of time in top water seeming to cloud attempts at understanding their migration, it may offer justification for their supposed absence of British waters. Furthermore, this discrepancy in time at depth between the sexes is something unreported in the literature thus far regarding the northwest Atlantic population.

During the creation of the species distribution model for *C. carcharias*, Figure 11 was produced. Although this mainly served to reinforce the literature, the influence exhibited by Chlorophyll (up to 25%) on habitat selection is something unreported in the literature thus far. Domeier *et al.*'s (2012) study looking at seasonal habitat use of Guadalupe island was one of the most thorough reports found, evaluating variables such as lunar cycles, dissolved oxygen and water turbidity. Having said this, even this report fails to look at the relationship Chlorophyll may have on habitat selection for this species.

C. carcharias is known to spend large amounts of time in water <20°C (Cliff, Dudley and Davis, 1989; Fergusson, 1996; Domeier and Nasby-Lucas, 2008, 2012; Bonfil *et al.*, 2010; Bruce and Bradford, 2012; Francis *et al.*, 2012, 2012). Figure 12, plot A suggests that this is not the case, adding to the literature eclipsing Cliff, Dudley and Davis' (1989) hypothesis; that 26°C is the upper limit of the GWS, stating that the highest habitat suitability can be found at values over 26°C. Furthermore, some of the lowest habitat suitability values are between 13 – 16°C; this is the average

summer SST for British waters. Although this finding, in conjunction with Figure 11, may provide evidence for the common idea that British waters are too cold for *C. carcharias*, it should be noted Figures 13 – 15 still show an exceedingly high habitat suitability across all seasons.

Figure 12, plot B shows waters above a Chlorophyll concentration of 0.50mg^{-3} have high habitat suitability, nevertheless, there are few marine habitats with Chlorophyll values $<0.25\text{mg}^{-3}$. Although this variable can have up to 25% impact on GWS habitat selection, Figure 12 merely shows that they do not frequent extremely oligotrophic environments. Furthermore, there seems to be an unexplained drop in habitat suitability near 0.40mg^{-3} of Chlorophyll. This is most likely due to noise within the data set as these plots were created with four tagged sharks worth of data - if this were to be repeated with 100 sharks this small fluctuation would be expected to be reduced. The deepest dive recorded by a tagged GWS was 1,200m (Francis *et al.*, 2012); Figure 12 plot C shows that this is the exact depth at which habitat suitability declines, yet these sharks can be found swimming in waters with a maximum depth of 5000m - this does not support Bruce and Bradford's (2012) aforementioned hypothesis as both sexes were recorded swimming in waters greater than their supposed threshold; meaning they could not reach the bottom to aid their migration.

Waters within close proximity to the study area's landmass show an exceedingly high; near uniform, spread of >0.95 habitat suitability all year round for both sexes. Interestingly the season displaying the greatest habitability was not summer, but spring; with values >0.98 across the whole study area. Despite having a higher mean temperature, summer exhibited a similar suitability to the other more temperate seasons, challenging the theory that GWS migration is temperature driven. Moreover, the areas of lower suitability are found below latitude 52° and between -5° to -15.5° longitude. Upon comparison to Figure 1, it can be denoted that these lower values are located off the continental shelf, Figure 12; plot C, indicates that this lower suitability is most likely a result of depth. These deeper, less inhabitable waters are situated in a manner that if a GWS from the north Atlantic or Mediterranean population were to travel to British waters, it would be these waters that they would first encounter, potentially deterring the individual.

When comparing the seasons, little differentiation in suitability between sexes can be seen. Both sexes are impacted more by bathymetry in summer and autumn as opposed to winter, where there is a clearer divide in spatiotemporal habitat suitability. This finding in winter suggests that GWSs may be sexually segregated due to the lower limits of thermal tolerance. Despite this lower boundary not being discussed in the literature regarding *C. carcharias* sexual segregation, thermal influences/limits are suspected to play a part in this phenomenon (Bruce *et al.*, 1996; Sims, Nash and Morritt, 2001; Domeier and Nasby-Lucas, 2012; Robbins and Booth, 2012). The findings of this report propose that females prefer cooler water, contradicting Robbin's and Booth's (2012) warmer water embryonic development theory, although it was unknown whether the two females tracked were pregnant.

Despite being one of the first of its kind, looking into a new seascape and using methodologies not extensively employed for the GWS before, this report has limitations. These include:

Number of sharks tracked

This report is based off the migrations of four mature individuals, two male and two female. This sample size is not large enough to create a holistic representation of the northwest Atlantic population. Furthermore, Nukumi's migration was only tracked for 12 months, yet it is known that females have a 24-month migratory pattern (Anderson, 2003; Domeier and Nasby-Lucas, 2012), therefore implying that 25% of migration data for females was not included in this study. Although the male's yearly migration was tracked, their pings were much more infrequent, potentially resulting in an underrepresentation of certain habitat conditions. Furthermore, all data is from mature sharks who have a different migration to younger individuals (Long *et al.*, 1996; Jorgensen *et al.*, 2012; Skomal *et al.*, 2017; Milankovic *et al.*, 2021). Increasing the minimum number of individuals tracked would increase the representation of the population, and therefore the validity of the results.

Lack of variables

Similar work by Austin *et al* (2019) on predicting habitat suitability for Basking sharks (*Centorhinus maximus*) examined 5 variables, and work by Elith *et al* (2008) looked at 11 environmental variables, furthermore, this report does not examine interior oceanographic variables such as underwater currents, thermoclines and pycnoclines. Although less is known about the drivers of GWS migration, additional environmental variables such as anthropologic activity, currents, predatory threats and interior oceanography may have illuminated a more definitive reason for their absence.

Missing data

SST and Chlorophyll-a data were recorded via remote sensing from MODIS-Aqua satellites. Resultantly, there are areas of the north Atlantic where Null values were recorded due to cloud cover and other environmental disturbances. Although this was accounted for when importing the data, it nevertheless resulted in fewer data being available, potentially leading to a less accurate model.

Unaccounted population

The main limitation of this report is its focus on the northwest Atlantic GWS population. Despite the study area being within this groups migratory range (Bonfil, 2005), it is not the closest population. It is much more probable that GWSs from the Mediterranean would frequent British waters purely due to proximity. The GWSs in the Mediterranean are an isolated population (Gubili *et al.*, 2011); not known to breed with others due to geographical constraints. This isolation can lead to the creation of ecotypes and eventually speciation (Quattro *et al.*, 2006). Therefore, the tracked individuals from the northwest Atlantic are likely to have different environmental preferences to those of the Mediterranean, thus basing the likelihood of GWSs frequenting British waters off the northwest Atlantic population's preferences disregards those of the more likely visitors from the Mediterranean. Though it is evident that data from Mediterranean individuals was desirable, tracking/migratory data for this population is extremely sparse, consequently the species distribution model was based off a more abundant data source.

No reason for the absence of *C. carcharias* from the British seascape was found using species distribution modelling with the suite of predictor variables used in this study. This suggests that there may be an ecological reasoning rather than

environmental. One of these ecological factors could be predation. Habitat selection based on predator avoidance has been documented within sharks (Morrissey and Gruber, 1993; Heupel and Simpfendorfer, 2005) and theorised to occur in GWSs (Bruce and Bradford, 2012). Despite being the apex predator in nearly all marine food chains (Estrada *et al.*, 2006; White *et al.*, 2019; Moro *et al.*, 2020), they can fall prey to the killer whale (*Orcinus orca*). Observations in the Pacific made by Weng (2007), showed that once orcas entered the same waters as GWSs, shark sightings dropped dramatically until the orcas left. As killer whales are commonly found in British waters, it is possible that they may be deterring GWS from entering these waters.

Anthropogenic activity is known to alter shark occurrence in a variety of ways (Kock *et al.*, 2018; Lagabrielle *et al.*, 2018; Moro *et al.*, 2020). This has led to the popular idea that boat traffic is deterring *C. carcharias* from British waters, yet case studies across a range of shark species indicate that boats can increase the occurrence of apex shark species due to their inquisitive nature and association with food (Fitzpatrick *et al.*, 2011; Sperone *et al.*, 2012; Gallagher *et al.*, 2014). Furthermore, GWSs are found in some of the busiest ports in the world such as San-Francisco (Anderson and Goldman, 1996), New York (Curtis *et al.*, 2018), and Busan (Choi, 2009), dispelling this theory.

C. carcharias is a philopatric species, often exhibiting site fidelity (Klimley, 1984; Bonfil, 2005; Domeier and Nasby-Lucas, 2008; Jorgensen *et al.*, 2010; Anderson *et al.*, 2011; Bruce and Bradford, 2012), this may explain why they are not in British waters, simply because they never have been. Yet, due to changes such as global warming, fishing pressures and food depletion, they may start venturing into uncharted waters to seek new food sources or waters with more favourable conditions (Thomas *et al.*, 2004; Pörtner and Knust, 2007; Dambach and Rödder, 2011; Bastien *et al.*, 2020).

Another more interesting theory, is that British waters are not visited by *C. carcharias* due to electromagnetics. As mentioned in section 1.3, the discovery that certain shark species use the earth's magnetic field as a map is very recent and poorly understood. It is currently unknown whether GWSs have this ability and if so, how this affects their migration. Thus, it is possible that their absence is due to British waters not possessing the correct electromagnetic parameters.

If the species distribution model produced in this investigation is accurate, then why has there yet to be a confirmed sighting of *C. carcharias* in British waters? As previously stated, the GWS is a sexually segregated species (Bres, 1993; Bruce *et al.*, 1996; Ferreira and Ferreira, 1996; Sims, Nash and Morritt, 2001; Domeier, 2012; Domeier and Nasby-Lucas, 2012; Francis *et al.*, 2012; Jorgensen *et al.*, 2012; Robbins and Booth, 2012; Milankovic *et al.*, 2021) and upon examination of Figures 8 – 9 it was seen that males travel long distances at depth and can go a year without surfacing. This suggests that if GWSs were to be inhabiting British waters, specifically males, then they may be spending a majority of time at depth, consequentially never being seen in surface waters. Whilst some of the literature would disagree with this idea; due to the GWS being a bimodal swimming species, much of this literature comes from the northwest Atlantic and Pacific populations, not the Mediterranean.

Conclusions

To understand why *C. carcharias* is not inhabiting British waters, species distribution modelling was employed through BRTs. A range of results were created displaying how each variable effects the shark's migration along with the overall suitability of the British seascape for the GWS. A general observation can be made that British waters show near perfect habitat suitability for *C. carcharias* all year round for both sexes. Therefore, the results of this report, in conjunction with the literature on this species, has produced two hypotheses:

1. Male GWSs are visiting British waters, but due to their bimodal behaviour they are not reliably seen and therefore have never been confirmed as being a species found in the study area.

Or

2. GWSs are not found in British waters as a result of the northwest Atlantic population exhibiting philopatry, thus never venturing this far from their known routes. Additionally, the Mediterranean population may have different environmental preferences, meaning that British waters are not as well suited to this closer population.

Although the pace at which new science being produced for elasmobranchs has never been higher, there is still much to learn about this species. Future work regarding habitat prediction and migration tracking of *C. carcharias* should begin with the tagging of the Mediterranean population, as they are the most likely population to undergo speciation. This could potentially introduce a whole new area of science regarding this species, whilst simultaneously aiding conservation efforts for this critically endangered population. Furthermore, all tags used should be able to record constant location and depth. This would give scientists a much better understanding of the species spatial-temporal habitat use.

Additional effort should also be made looking into the mystery of *C. carcharias* reproductive activities, as this is nearly certain to have a dramatic effect on habitat use and preferences for all populations.

Although the GWS may not be in British waters now, this species is currently experiencing a latitudinal shift north in habitat suitability due to climate change (Thomas *et al.*, 2004; Bastien *et al.*, 2020), indicating that if *C. carcharias* is not in British waters yet they may soon be.

Acknowledgements

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